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THE WINGS OF INSECTS.

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CHAPTER IV (*continued*).

The Specialization of Wings by Addition.

III. THE VENATION OF THE WINGS OF ODONATA.

THE wings of dragon flies have furnished the best of systematic characters since the days of Linnæus. The many peculiarities of venation have been slowly worked out and expressed in a formidable system of terms, most of which designate parts bearing other names in other orders. Indeed, this is not strange; for, from the study of the adult wings alone, the discovery of the real homologies would be well-nigh impossible.

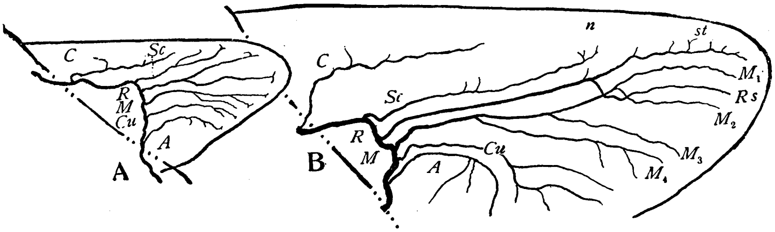

FIG. 60. — Wings of nymphs of *Gomphus descriptus*, early stages.

The richly veined wing of a dragon fly, at first sight, shows little in common with our hypothetical type. And even when the tracheation of the wing of an old nymph is studied, there are found some striking discrepancies. But in the budding wing of a young nymph we find an arrangement of the tracheæ which is almost that of the typical wing.

Fig. 60 represents the tracheation of two nymphs of *Gomphus descriptus*. The wing figured at *A* was only 1 mm. in length. Here is a costa with some anterior twigs, a subcosta with a terminal fork, a radius with its sector unbranched, a three-branched media, a cubitus which is two-branched in the usual way, and a single anal vein with three branches, which may represent the three anal veins, fused at the base.

At *B* (Fig. 60) is represented the tracheation of a somewhat older wing, one measuring 3 mm. in length. Here the radial sector has shifted its position and lies across the end of the media, the terminal portion of it lying between M_1 and M_2. The media is now four-branched. The costal and anal tracheæ are outrun by the others in the occupation of the new territory formed by the growth of the wing, and remain relatively short.

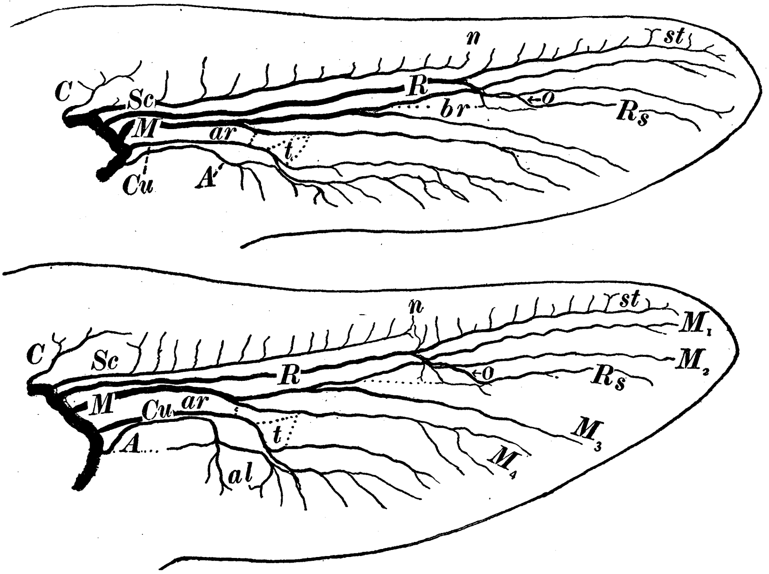

FIG. 61. — Fore and hind wings of a nearly grown nymph of *Cordulegaster diastatops*, showing tracheæ. *n*, nodus; *st*, stigma; *o*, oblique vein; *br*, bridge; *ar*, arculus; *t*, triangle; *al*, anal loop. The permanent venation which shows distinctly at this stage is omitted, except where indicated by dotted lines at the bridge, arculus, and triangle.

In the wings of a grown nymph (Fig. 61) is seen the culmination of these tendencies. The radial sector has completed its migration and lies in its final position, the terminal portion traversing the area between M_2 and M_3. The costa is greatly reduced or, rather, outstripped by its competitors; the same is true in a less degree of the subcosta and the anal vein. At this stage the veins, which are not represented in the figure, appear as pale, brownish thickenings; surrounding all of the principal tracheæ, and also surrounding the anastomosing tracheoles, which tend to group themselves in the positions of the cross-veins.

The most anomalous thing seen here is the position of the radial sector, a character which is quite distinctive of this order. In the adult wing (Fig. 62) this sector appears to be a branch of the media, and it has always been so interpreted. The only indication of its connection with the radius is the persistent obliquity of an apparent cross-vein between veins M_2 and R_s, just beyond the nodus.

The crossing of these tracheæ (Fig. 61) was first figured (incidentally) by Roster;[1] later it was described and discussed by Brauer and Redtenbacher;[2] and it was again figured and described by Brogniart.[3] But the effect of this crossing upon the homologies of the veins seems to have been overlooked. The apparent cross-vein is, in fact, a part of the radial sector; the longitudinal trunk connecting the sector with the media is not homologous with any of the principal veins, but is a secondary structure, developed for mechanical advantage, and the radial sector itself should be so termed, notwithstanding it appears to be a branch of the media and is far removed from

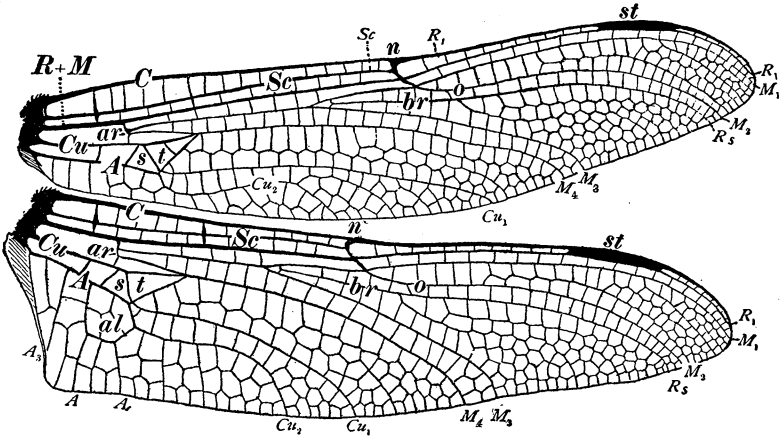

FIG. 62. — Adult wings of *Cordulegaster sayi*, lettered as in Fig. 61.

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[1] Roster, D. A. *Bull. Soc. Ent. Ital.*, vol. xvii (1885), Pl. IV.

[2] Brauer u. Redtenbacher. *Zool. Anz.*, Bd. xi (1888), pp. 443–447.

[3] Brogniart. *Recherches sur les Insectes Fossiles* (1894), pp. 204–208, Pl. VIII.

its usual position. It will be convenient to designate that part of the radial sector which appears as a cross-vein behind vein M_2 as the *oblique vein* (Fig. 62, *o*); and the secondary longitudinal trunk as the *bridge* (Fig. 62, *br*).

In the adult wing the bridge exhibits no evidence of an origin different from that of the radial sector, with which it is strictly continuous. But a study of the tracheation of the wings of nymphs reveals the secondary nature of the origin of the bridge. Fig. 63 is a reproduction of a photograph of a portion of a wing of a nymph of *Anax junius*, showing the crossing of the radial sector, and the origin of the trachea which precedes the bridge. The latter is a small twig which arises from the distal end of that portion of the radial sector which becomes the oblique vein, and extends towards the base of the wing in a direct line to the media. This method of formation of the bridge is characteristic of the Æschnidæ.

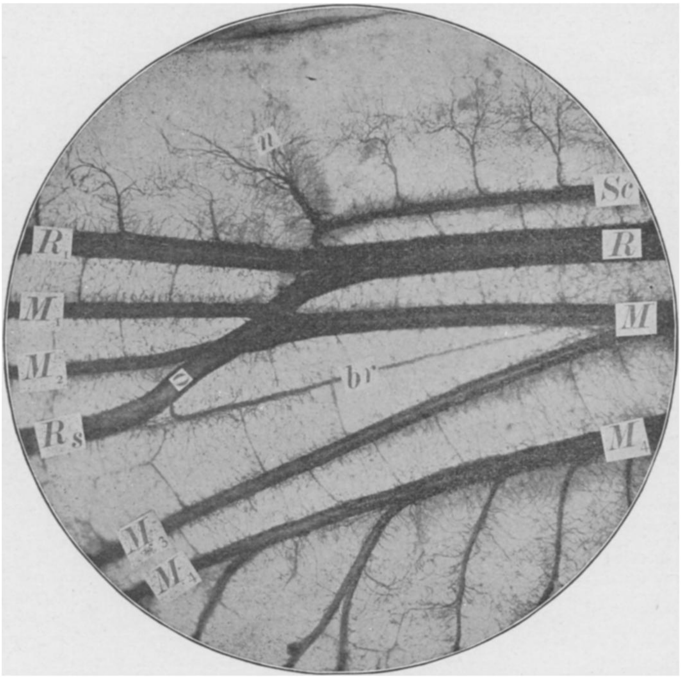

FIG. 63.—The region of the nodus in *Anax junius*, showing the crossing of the radial sector and the origin of the trachea which precedes the bridge. *o*, oblique vein; *br*, the bridge.

In most Libellulidæ a trachea, or a bunch of tracheoles, descends from near the base of the radial sector and forks at the level of the bridge, one branch going to the distal end of the oblique vein, the other going in a diametrically opposite direction to the media (Fig. 64).

The illustrations just given exhibit the structure of these parts in nymphs of the suborder Anisoptera. In the suborder Zygoptera (Calopterygidæ and Agrionidæ) there exists a striking difference. If we compare adult wings of the two suborders, there can be no question as to the identity of vein R_s, or as to its homology in the two groups. But in the suborder Zygoptera, so far as known to us, the trachea R_s is a branch of the medial trachea. The base of R_s, however, forms an oblique vein, and a bridge is developed secondarily, as in the Anisoptera. It is probable that there has been a switching of the base of the trachea R_s from trachea R to trachea M. One has only to examine a well-mounted wing of any dragon-fly nymph to see in the universal anastomoses of tracheoles communications already set up between principal tracheæ, any one of which

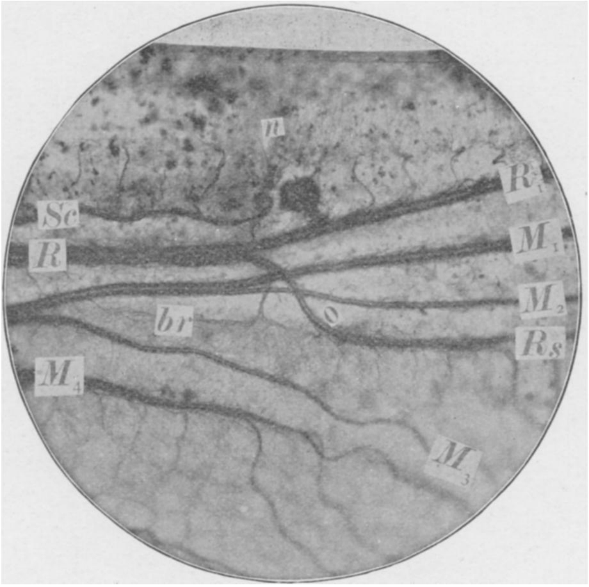

FIG. 64. — The region of the nodus in *Libellula pulchella*. *o*, oblique vein; *br*, the bridge.

might be enlarged, should necessity arise for the entrance of air from a new quarter. Following this, the atrophy of the old connection would complete the switching; which, we believe, is what has happened in the Zygoptera. It follows from this that, so far as this portion of the wing is concerned, the Zygoptera depart more widely from the primitive type than do the Anisoptera. From this brief sketch it is evident that these parts will furnish systematic characters which are as yet unused.

For increasing its efficiency, certain methods of bracing the dragon-fly wing in its costal and basal parts have been perfected to a degree surpassing anything to be seen in any other order. The veins of the costal margin are thickened and approximated as usual; but the strong corrugation of the area traversed by them is maintained by their being bound together at the nodus, at the stigma, and often toward the base, where certain of the antenodal cross-veins become greatly thickened. These hypertrophied antenodals sometimes (as in Æschna) become stout triangular trusses which completely fill, in section, the furrow between the costa and the radius. Toward its base, the wing is braced by two characteristic structures well known in the literature of the Odonata as the *arculus* and the *triangle*. The arculus has already been discussed.[1]

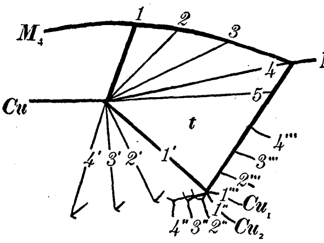

Fig. 65.— Diagram setting forth the behavior of the triangle in the suborder Anisoptera. The heavy lines bound a somewhat primitive triangle. 2, 3, 4, and 5 are stages in the descent of the upper cross-vein which are to be seen in such living genera as Tetrathemis, Anatya, Libellula, and Tetragoneuria, respectively. 1', 2', 3', and 4' represent successive stages in the retraction of the cubitus at the triangle, stages seen in the fore wings of Microdiplax, Anatya, Sympetrum, and Perithemis, respectively. 1'', 2'', 3'', and 4'' represent stages in the retraction of the base of vein Cu_2 as seen in the fore wings of Orchithemis, Anatya, Libellula, and Tetragoneuria. 1''', 2''', 3''', and 4''' represent stages in the ascent of the vein Cu_1 up the outer side of the triangle, stages seen in the hind wings of Ladona, Mesothemis, Anatya, and Nannodythemis.

The Triangle.— The deflection of the cubital trachea, just before its fork, makes a place for the development of the triangle. This is one of the most important features of the wings in the suborder Anisoptera, to which alone the following remarks will apply. While its stout boundaries unite strongly the three posterior longitudinal veins, only its inner side is bounded by a principal vein, its anterior and outer sides being formed from two cross-veins approximated upon vein M_4. Primitively it differed little from an ordinary rectangular cell. The accompanying diagram (Fig. 65) shows the successive positions assumed by its anterior and inner sides and by the two branches of the cubitus at their departure from it. This epitome of its history presents only steps in its development that are still preserved in the wings of living genera.

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[1] *American Naturalist*, vol. xxxii, No. 376, p. 234, Fig. 7.

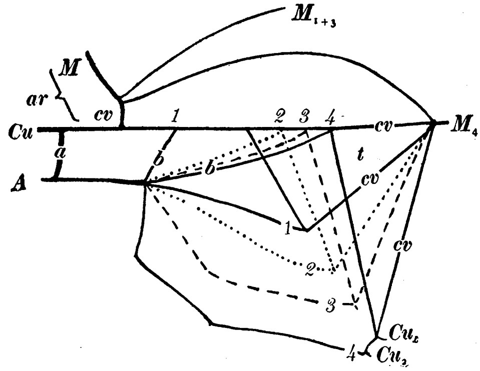

Fig. 66. — Diagram illustrating the procession of the triangle, and the deflection of the second Cu-A cross-vein in the fore wings of Libellulidæ. *a*, the first, and *b*, the second Cu-A cross-veins; 1, 2, 3, and 4, successive positions.

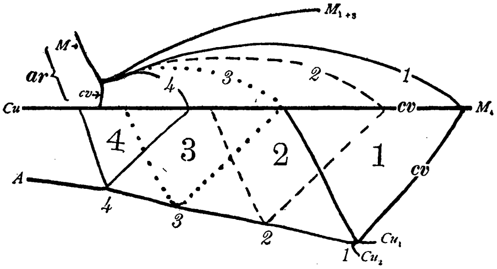

Fig. 67. — Diagram representing the recession of the triangle in the hind wings of the Libellulidæ. 1, 2, 3, and 4, successive stages.

In the Libellulidæ differentiation between fore and hind wing has changed the relation between arculus, triangle, and anal vein. Doubtless these were once similarly placed in the two wings, the triangle being a little beyond the arculus, and the anal vein meeting its hind angle in both wings (as, for instance, at present in Cordulegaster). In the fore wing the anal vein has come to connect with the antero-internal angle of the triangle through the deflection of the second cubito-anal cross-vein, and the triangle has proceeded farther from the arculus. Successive steps are shown in the accompanying diagram (Fig. 66). In the hind wing the triangle has receded to the level of the arculus, or even a little farther, by the easy stages shown in the accompanying diagram (Fig. 67), and the second cubito-anal cross-vein has atrophied.

The Anal Loop. — There is also in the Anisoptera a strong tendency toward the development in the hind wing of a broadly expanded anal area — an aëroplane. This region remains still unexplored territory. It will furnish, however, at least one character of much systematic importance. This is a space included between the first and second principal branches of the anal vein, which we designate as the *anal loop*. Its development is shown in Fig. 61. When developed in the Æschnidæ as a distinct enclosure, it is always compact in form, but in the more specialized of the Libellulidæ it becomes elongate, then gland-shaped, and then foot-shaped. Fig. 68 shows its more characteristic forms, and gives an idea of its variability within the group.

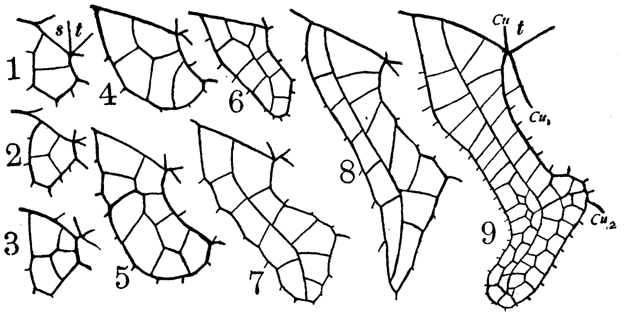

FIG. 68. — Forms of the anal loop in the Anisoptera: 1, anal loop of *Cyclophylla diphylla*; 2, of *Gomphoides stigmatus*; 3, of *Gomphæschna furcillata*; 4, of *Gomphomacromia paradoxa*; 5, of *Syncordulia gracilis*; 6, of *Agrionoptera insignis*; 7, of (?) *Nannophya maculosa*; 8, of *Ephidatia longipes*; 9, of *Hydrobasileus extraneus*.

We have now indicated the homologies of the principal veins: we have briefly discussed the development of a few of the distinctive venational characters of this interesting group;

there is not space for details, but these are the less necessary because the junior author will shortly publish elsewhere an extended paper upon the venation of this order. It may be remarked, however, in passing, that the tendency throughout the order is toward vein multiplication. Additions are made upon both sides of several principal branches, and they conform to no one simple type. These new branches are preceded by tracheæ; but there are other interpolated veins developed for mechanical advantage quite independently of the tracheæ and cutting across them.

The radial sector is unique in form as well as in position.

All the peculiarities of this intricate venation have arisen out of the necessity for making all the veins individually useful: and those dragon flies which have been most successful in differentiating between the added veins are among the fleetest of winged creatures.